OLD FIELD SUCCESSION IN MOJAVE DESERT SCRUB

DEAN E. CARPENTER
Environmental Science and Engineering, University of California,
Los Angeles 90024

MICHAEL G. BARBOUR[1]
Department of Botany, University of California,
Davis 95616

CONRAD J. BAHRE
Department of Geography, University of California,
Davis 95616

ABSTRACT

Secondary (old field) succession in Mojave Desert scrub vegetation was studied in 20 abandoned homestead fields in the uplands of the eastern Mojave Desert, California. The fields, which were last plowed between 1913 and 1930, were stratified equally in three vegetation types: creosote bush scrub (1100 m elevation), Joshua tree grassland (1280 and 1430 m), and sagebrush/juniper scrub (1615 m). Cattle grazing has been the only widespread disturbance since the fields were abandoned. Our investigation of cover and size of perennial plants indicated that secondary succession in creosote bush scrub is approaching climax (off-field conditions) within approximately 65 years, but that succession in vegetation at higher elevations may require many more years.

Succession in deserts is little understood and little studied. Since the work of Shreve and Hinckley (1937), no studies have been done on long-term succession in the deserts of the American Southwest. This is true especially for the Mojave Desert. Rowlands (1980) reviewed studies of revegetation and disturbance there, and found only a few, all completed since 1961. Those studies involved primarily creosote bush scrub in relation to ghost towns (Wells 1961, Webb and Wilshire 1980), energy corridors (Vasek et al. 1975a), pipeline construction sites (Vasek et al. 1975b), freeways (Vasek 1979), and off-road vehicle impacts (Davidson and Fox 1974). Recently, Prose and Metzger (1985) studied succession on abandoned World War II military training camps in the region.

In the present study, our objective was to document secondary (old field) succession in an array of Mojave Desert vegetation types at several elevations. Abandoned homestead fields in the uplands of the eastern Mojave Desert of California offer an ideal opportunity to accomplish this, because the fields have been relatively undis-

[1] Request reprints from Michael G. Barbour, Department of Botany, University of California, Davis, CA 95616.

MADROÑO, Vol. 33, No. 2, pp. 111–122, 30 May 1986

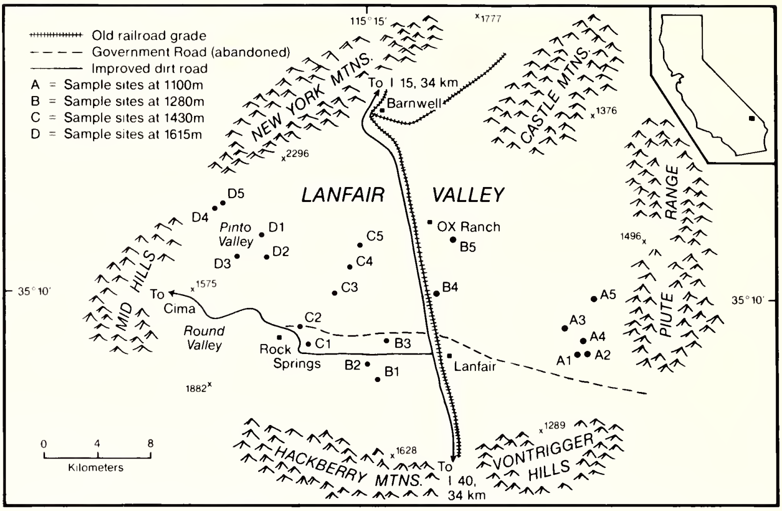

FIG. 1. Map of Lanfair Valley.

turbed since they were abandoned nearly 65 years ago (Carpenter 1983). The fields are located in the Lanfair Valley about 50 km northwest of Needles and range in elevation from 1090 to 1670 m. For the most part, they have similar soils, slope aspects, and slope gradients. Cattle grazing has been the only widespread disturbance since the fields were abandoned. Our hypothesis was that sufficient time had elapsed since these fields were abandoned to permit us to quantify long-term revegetation dynamics by Mojave desert scrub, and to estimate time required to reestablish climax vegetation.

STUDY AREA

Physical setting. Lanfair Valley, which is about 32 km in diameter, is bordered on the west and north by the Mid Hills and the New York Mountains and on the south and east by Hackberry Mountain and the Piute Range (Fig. 1). The valley floor is covered by alluvium and dips in elevation from about 1720 m in the northwestern part near the New York Mountains to 1005 m in the southeastern part.

Bard (1972) estimated that average annual precipitation ranges from 180 mm to 250 mm, with the greatest amounts at the highest elevations. The precipitation pattern is biseasonal: two-thirds falls between December and March, and the remaining third falls between July and September. Daily high temperatures in the summer are typically 32–37°C but occasionally approach 49°C (Bard 1972). Winter temperatures are cool, with occasional minimum temperatures of about −18°C.

The major vegetation types of the valley are (from lowest to highest elevations) creosote bush (*Larrea tridentata*) scrub, Joshua tree (*Yucca brevifolia*) grassland (*sensu* Johnson 1976), and sagebrush (*Artemisia tridentata*)/juniper (*Juniperus osteosperma*) scrub (Munz 1959, Vasek and Barbour 1977). Grasses (C_4 type) are particularly abundant in all these types.

Land-use history. Except for a few hunting-and-gathering Chemehuevi Indians (Miller and Miller 1967, Laird 1976), the Lanfair Valley was largely unsettled until Anglo ranchers moved into the valley in 1880 (Carpenter 1983, Hewett 1956). At that time, now-scarce grama grass (*Bouteloua*) covered the valley "as far as the eye could see" (Foreman 1941, Casebier 1974). The first farmers homesteaded in the valley in 1910 and attempted to dry-farm milo, corn, and beans (Thompson 1929, Gilman 1977). Dry farming failed, however, and new settlers moved into the valley and obtained public land at nominal cost through either the Desert Entry Law or the Homestead Law (U.S. BLM 1971). Those laws required the homesteaders to plow part of their land for crops, even though the fields did not necessarily have to produce a harvest. Most of the homesteads were not "proved up," however, and the claims, with their once-plowed fields, were soon abandoned.

The number of homesteaders was once large; in 1917, 130 registered voters and their families were reported in Lanfair Valley (Thompson 1929, Carpenter 1983). By 1926, however, only nine people lived in the valley (Hewett 1956). Since then, the population has remained low and livestock grazing has been the major economic activity.

Methods

Seventy-five abandoned homestead fields were identified in large-scale color aerial photographs of Lanfair Valley taken in 1974. Twenty of these fields, divided among four elevation belts (1100 m, 1280 m, 1430 m, and 1615 m) corresponding with vegetational belts, were selected for study and interpolated from the aerial photographs onto 15′ USGS topographic quadrangles. Bureau of Land Management plat records and National Archive documents were used to estimate the years in which the fields were last plowed (Table 1).

Surveys of perennial and dominant plants were conducted in November–December 1982 to quantify differences in plant composition between the abandoned homestead fields and adjacent unplowed areas. For the perennial plant survey, a randomized plot method was used to measure the density, cover, and frequency of each species. A transect line, perpendicular to topograhic lines, was established across the maximum length of each field. Fourteen sample plots, each 4 m^2 in size, were placed randomly along the transect line of the perennial plant survey: 10 plots at least 50 m inside the

TABLE 1. HOMESTEAD FIELD CHARACTERISTICS. Density of dominants is for the surrounding, undisturbed vegetation.

Elevation belt (m) and density of dominants	Site (see Fig. 1)	Elevation (m)	Area (ha)	Year last plowed
1100, *Larrea,* 270 ha^{-1}	A1	1091	22	1921
	A2	1091	9	1921
	A3	1116	15	1921
	A4	1097	7	1930
	A5	1116	13	1913
1280, *Yucca,* 82 ha^{-1}	B1	1274	22	1916
	B2	1311	13	1918
	B3	1292	9	1915
	B4	1274	23	1917
	B5	1268	34	1914
1430, *Yucca,* 67 ha^{-1}	C1	1402	8	1917
	C2	1426	20	1919
	C3	1433	8	1917
	C4	1433	19	1918
	C5	1430	10	1920
1615 *Artemisia,* 750 ha^{-1}	D1	1609	19	1923
Juniperus, 26 ha^{-1}	D2	1561	22	1924
	D3	1585	25	1924
	D4	1670	10	1924
	D5	1664	14	1924

field boundaries (on-field), and four plots at least 50 m outside the field boundaries (off-field). Fewer plots were chosen for off-field vegetation sampling because of the apparent homogeneity in the vegetation, whereas 10 plots were thought necessary to sample gradients in vegetation density from field edges to field centers. Dominant species were not sampled in the plots.

A point-quarter method was chosen for the dominant plant survey (Cottam and Curtis 1956). Because the first transect line placed off-field sampling points too far from the fields, an additional transect line was required to sample adjacent unplowed areas for this survey. This second line was placed either parallel or perpendicular to the transect line of the perennial plant survey (depending on field area); its starting point was 50+ m outside the field boundary. In addition to distance measures along the transects, the maximum diameter of each creosote bush and the height of each Joshua tree were recorded to the nearest 0.5 m in the dominant plant survey.

The Student's t-test was used in the individual-site analysis to compare the on-field and off-field mean cover values of a species. Independent samples and equal variances were assumed for the on-field and off-field populations when using the t-test. The aggregate sample variance was skewed because the numbers of sample plots were unequal (10 on-field and 4 off-field) (Steel and Torrie 1980).

Because cover was a proportional measure and most values were less than 30%, cover data were converted by an angular transformation. This transformation ensured the *t*-test's requirements of normally distributed data. The *t*-test also was used to compare density and width/height means of dominant species at individual sites on-field and off-field.

In order to detect vegetational differences between the plowed and unplowed areas, the five most important off-field perennials and the five most important on-field perennials were selected at each sampled elevation as representative species. A species importance value (I.V., the sum of relative density, cover, and frequency; maximum value of 300) was used to select the representative species and later to compare plowed and unplowed areas.

RESULTS

Distribution of the dominants Larrea and Yucca. Larrea tridentata was the dominant species at off-field 1100 m elevation sites, and *Yucca brevifolia* was the aspect dominant at the intermediate elevations. These two species differed in their ability to invade the abandoned fields. *Juniperus osteosperma* was the potential aspect dominant in the 1615 m elevation belt, but its low density and continuous disturbance (harvesting) in this century made it impossible to compare its behavior on- and off-field.

Larrea density averaged 270 plants ha^{-1} off-field, and those plants had an average diameter of 1.81 m, for an absolute cover of 6.8%. On-field, *Larrea* density averaged 155 plants ha^{-1}, plant diameter was 1.30 m, and absolute cover was 2.0%. Three of the five paired locations showed significant differences in density, and two of the five showed significant differences in shrub diameters.

Yucca density averaged 75 plants ha^{-1} off-field, and those plants had an average height of 2.37 m. In most cases, *Yucca* reestablishment was very slow. On-field, site C-3 exhibited a *Yucca* density ($P < 0.01$) not significant from off-field. On-field, site B-3 had about ⅕ the density of *Yucca* as off-field. No other on-field site showed more than 0.5 *Yucca* plants ha^{-1} and these differed significantly from off-field sites ($P < 0.01$). For the C-3 and B-3 sites, *Yucca* heights on- and off-field were not statistically different.

The fields that showed the least difference in *Larrea* or *Yucca* abundance, compared with the off-field pairs, were those of smallest size and narrowest dimensions (Carpenter 1983).

Distribution of the 10 associated species. Fifty perennial species, in 16 families, were present in the 20 paired sites. Species richness in both on- and off-field sites increased with elevation from 1100 to 1430 m, then fell at 1615 m (Fig. 2). Except at the lowest ele-

TABLE 2. THE 10 MOST IMPORTANT ASSOCIATED PERENNIAL SPECIES AT THE FOUR SAMPLED ELEVATIONS. CR = cover ratio, the ratio of average on-field cover to average off-field cover.

Species	Code	CR
Leucelene ericoides	LEER	12.00
Sphaeralcea ambigua	SPAM	3.27
Acamptopappus sphaerocephalus	ACSP	2.10
Hymenoclea salsola	HYSA	1.69
Gutierrezia microcephala	GUMI	1.51
Lycium andersonii	LYAN	1.17
Haplopappus cooperi	HACO	0.97
Hilaria rigida & H. jamesii	HISP	0.81
Artemisia tridentata	ARTR	0.40
Ephedra nevadensis	EPNE	0.08

TABLE 3. IMPORTANCE VALUES OF THE 10 LEADING ASSOCIATED PERENNIAL SPECIES THAT OCCURRED AT EACH ELEVATION. (Refer to Table 2 for an explanation of species codes.)

Elevation belt (m)	Code	Off-field	On-field
1100	ACSP	41	30
	GUMI	42	7
	HISP	113	92
	HYSA	5	14
	LYAN	23	19
	SPAM	25	87
	Others	51	52
1280	EPNE	14	7
	GUMI	37	43
	HACO	50	59
	HISP	68	50
	HYSA	34	66
	LYAN	9	10
	SPAM	10	23
	Others	78	43
1430	EPNE	11	1
	GUMI	34	53
	HACO	27	23
	HISP	33	38
	HYSA	23	42
	LEER	35	51
	SPAM	10	25
	Others	126	67
1615	ARTR	55	29
	EPNE	18	2
	GUMI	95	92
	HISP	38	19
	LEER	12	62
	SPAM	17	15
	Others	65	83

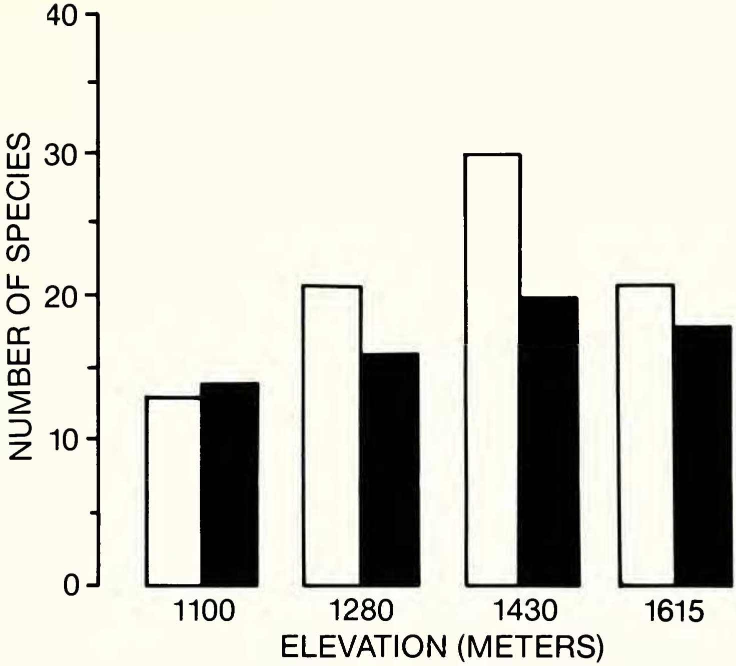

FIG. 2. Off-field (white) and on-field (dark) perennial species richness for stands in the four elevation belts.

vations, off-field sites had about 20% more species per unit area than paired on-field sites. These patterns, however, were not statistically significant.

Perennial cover generally varied between 20 and 30%, and no pattern of increase correlated with elevation. On-field cover was lower than paired off-field cover at all but the lowest elevations where the reverse was true. Cover was significantly different between paired sites, however, only in the 1430 m elevation belt. In general, on-field cover was not significantly different from off-field cover.

Importance values (I.V.s) were calculated for the five leading species from the pooled collection of species found on-field and for the five leading species from the pool of species found off-field. The 10 species (Table 2) included such taxa as *Leucelene ericoides,* which exhibited an overwhelming preference for on-field sites; *Haplopappus cooperi,* which was equally abundant on- and off-field; and others such as *Ephedra nevadensis,* which was skewed to off-field sites. Throughout the range of elevations, the five off-field species accounted for 58–83% of cumulative I.V.s, and the five on-field species accounted for 72–86% of cumulative I.V.s.

At 1100 m, *Hilaria* was the overwhelming plant off-field, with an I.V. twice that of the next most important species (Table 3), whereas on-field it shared importance with *Sphaeralcea. Sphaeralcea* and *Hymenoclea* were three times more important on-field than off-field. *Gutierrezia,* in contrast, dropped in importance from second place off-field to a distant sixth place on-field.

At 1280 m, *Hilaria* was again dominant off-field, but less overwhelmingly so, and it was third in importance on-field (Table 3). *Hymenoclea* and *Sphaeralcea* roughly doubled in importance on-field as compared with off-field. *Haplopappus, Gutierrezia,* and *Lycium* were almost equally important off- and on-field.

At 1430 m, *Leucelene* and *Gutierrezia* had the leading I.V.s both off- and on-field, but dominance was rather closely shared with two or three other species (Table 3). *Hymenoclea* and *Sphaeralcea* again doubled in importance on-field compared with off-field. *Ephedra* dropped in I.V. from 10 off-field to one on-field.

At 1615 m, *Gutierrezia* was the most important plant both off- and on-field (Table 3). The I.V.s of *Artemisia* and *Hilaria* dropped by half on-field compared with off-field, and that of *Ephedra* dropped from 18 to two. In contrast, the I.V. of *Leucelene* increased five-fold on-field compared with off-field. This was the only elevation belt at which "other species" had a collective I.V. greater on-field than off-field, indicating that species richness was greater on the disturbed sites.

In summary, characteristic associated plants that responded positively to past disturbance were *Leucelene, Sphaeralcea, Hymenoclea,* and *Gutierrezia. Acamptopappus, Lycium,* and *Haplopappus* had no strong response. *Hilaria, Artemisia,* and *Ephedra* responded negatively. Absolute cover values for the 10 species paralleled the I.V. patterns (Fig. 3).

Discussion

Undisturbed sites at the 1100 m elevation were dominated by a relatively dense cover of *Larrea,* 2–3 m tall; understory was predominantly *Hilaria,* although *Acamptopappus, Gutierrezia,* and *Lycium* were important understory shrubs. Some 65 years following disturbance, on-field sites showed significant invasion by *Larrea*: in the majority of cases density, cover, and canopy size were statistically equal to those in control, off-field sites. The sub-shrub *Sphaeralcea* and the shrub *Hymenoclea* were the most important associated plants. *Acamptopappus* and *Lycium* were also present, with I.V.s similar to those of off-field sites. In fact, only eight species found on- and off-field showed significant cover differences (Fig. 3), and as a result, field boundaries were sometimes difficult to identify. Species richness differed only 20% between on- and off-field sites.

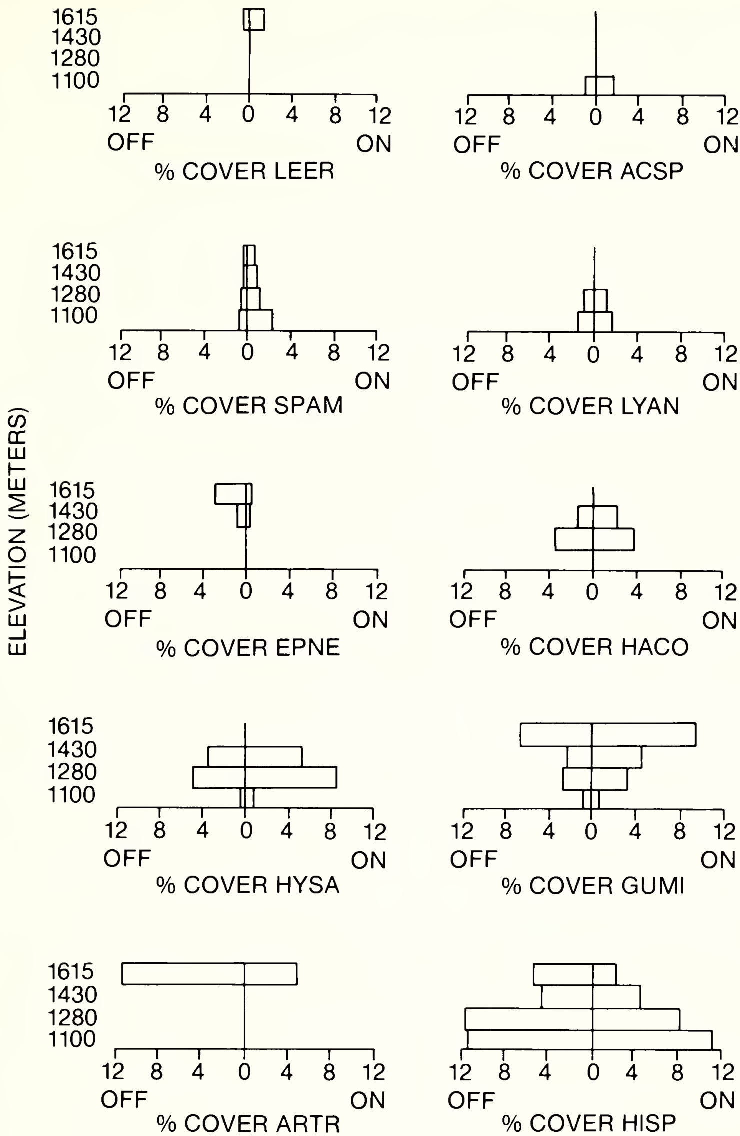

FIG. 3. Off-field (left) and on-field (right) absolute cover for the 10 most important associated perennial species at all four elevations. No LEER or ACSP paired-sites showed significant cover differences (*t*-test) on- or off-field. The other eight taxa showed significant differences in cover on- and off-field for at least some of the sites. (Refer to Table 2 for an explanation of species codes.)

Undisturbed sites at the 1280 and 1430 m elevations were dominated in aspect by *Yucca brevifolia,* 2–4 m tall, sometimes associated with other arboreal species, *Y. schidigera* and *Opuntia acanthocarpa. Hilaria* was among the most important associated plants, as were *Gutierrezia, Haplopappus,* and *Leucelene.* Nearly 70 years following disturbance, on-field sites exhibited virtually no arboreal species. *Hymenoclea* was the dominant, associated with *Sphaeralcea, Gutierrezia,* and *Leucelene.* There was significantly less total cover on-field than off-field, and 23% of all species showed significant differences in cover ($P < 0.05$). Species richness was lower on-field than off-field. In contrast to creosote bush scrub, Joshua tree grassland was far from reaching predisturbance composition.

Undisturbed sites at the 1615 m elevation were dominated in aspect by *Juniperus,* 2–4 m tall, especially near washes. *Opuntia acanthocarpa* was also present in the overstory. *Gutierrezia* and *Artemisia* were the dominant shrubs, and *Ephedra* and *Yucca baccata* were commonly associated. Grasses were less important in the understory than at lower elevations. Nearly 65 years following disturbance, on-field sites had virtually no arboreal species. *Artemisia* was significantly reduced in importance. The dominants were *Gutierrezia* and *Leucelene,* and species richness was lower than on undisturbed, off-field sites. Some 37% of all species showed significant cover difference on-field and off-field (Carpenter 1983). Thus sagebrush/juniper scrub had progressed even less toward regaining predisturbance composition than had Joshua tree grassland.

Secondary succession at the lowest elevations (creosote bush scrub) is apparently approaching climax (the conditions of the off-field grazed vegetation) within a time span of approximately 65 years, but succession at the higher elevations (Joshua tree grassland and sagebrush/juniper scrub) may require twice as many years. The rate of succession is probably confounded by the impact of cattle in this century, and we cannot with certainty estimate what the course or time of secondary succession would have been in its absence.

Although Shreve (1942) stated that succession does not occur in deserts, evidence accumulated since that time suggests that both primary succession (Vasek and Lund 1980) and secondary succession can occur in the Mojave Desert. Prose and Metzger's (1985) very detailed study of tent sites, roads, and parking lots in a tank training area abandoned for 40 years, divided perennial shrubs into three categories: long-lived, long-lived opportunistic (only one species, *Ambrosia dumosa*), and short-lived. On disturbed sites, long-lived perennial cover was significantly less than that of undisturbed controls, but cover by the other two categories of shrubs was greater than that of controls. Long-lived perennials included species of *Atriplex, Encelia, Krameria, Larrea, Opuntia, Dyssodia, Encelia, Hymenoclea, Porophyllum,* and *Stephanomeria.* Recovery of long-lived perennials correlated negatively with the magnitude of soil compaction. Their estimates of time necessary to achieve climax ranged from just less than 50 years to over 550 years.

Wells (1961) also showed that secondary succession proceeds through a seral stage of short-lived perennials. Streets abandoned for 30 years in a mining town were dominated by an open stand of bunchgrass (*Stipa*) and short-lived subshrubs (*Hymenoclea, Salazaria,* and *Thamnosma*)—taxa normally restricted to dry washes. The only substantial densities of long-lived perennials were species of stump-sprouting *Lycium* and *Ephedra.* Adjacent undisturbed sites showed densities of long-lived perennials (*Grayia* and *Larrea)* 20-fold greater than on disturbed sites. Wells gave no estimate of recovery time to climax, but clearly 30 years was far too brief.

Vasek et al. (1975a) examined desert scrub beneath powerlines that were 30 years old and reported an increase in cover by short-lived perennials such that total cover was greater than that of adjacent, undisturbed areas. Pipeline corridors, disturbed 12 years in the past (Vasek et al. 1975b), showed long-lived perennial cover only 0–41% that of controls, and Vasek estimated that the time to reestablished climax there may be 40 years. His observations (Vasek 1979) of an eight year old barrow pit, however, led him to conclude that succession would require "a few centuries." In all of these, a seral stage of short-lived, suffrutescent perennials was apparent.

Our work on old field succession suggests that a similar seral community of short-lived perennials invades and is replaced slowly by increasing populations of long-lived climax shrubs. In our sites, the most prevalent short-lived species were *Leucelene ericoides, Sphaeralcea ambigua, Acamptopappus sphaerocephalus, Hymenoclea salsola,* and *Gutierrezia microcephala,* which had cover values 2–20 times that of undisturbed sites. Our estimate of 65–130 years required for establishment of predisturbance vegetation cover is well within the estimates reported above for other types of disturbance.

Literature Cited

Bard, R. C. 1972. Settlement pattern of the eastern Mojave Desert. Ph.D. dissertation, Univ. California, Los Angeles.

Carpenter, D. E. 1983. Old-field succession in Mojave Desert scrub. M.S. thesis, Univ. California, Davis.

Casebier, D. G. 1974. Fort Pah-Ute, California. Tales of the Mojave Road Publ. Co., Norco, CA.

Cottam, G. and J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. Ecology 37:451–460.

Davidson, E. and M. Fox. 1974. Effects of off-road motorcycle activity on Mojave Desert vegetation and soil. Madroño 22:381–412.

Foreman, G. 1941. A pathfinder in the southwest—the itinerary of Lieutenant A. W. Whipple during his explorations for a railway route from Fort Smith to Los Angeles in the years 1853 & 1854. Univ. Oklahoma Press, Norman.

Gilman, H. F. 1977. The origin and persistence of a transit region: eastern Mojave Desert of California. Ph.D. dissertation, Univ. California, Riverside.
Hewett, D. F. 1956. Geology and mineral resources of the Ivanpah Quadrangle, California and Nevada. U.S.G.S. Prof. Paper No. 275. U.S. Gov. Printing Office, Washington.
Johnson, H. B. 1976. Vegetation and plant communities of southern California deserts—a functional view. *In* J. Latting, ed., Symposium proceedings, plant communities of southern California, Spec. Publ. No. 2, p. 125–164. California Native Plant Society, Berkeley.
Laird, C. 1976. The Chemehuevis. Malki Museum Press, Banning, CA.
Miller, R. D. and P. J. Miller. 1967. The Chemehuevi Indians of southern California. Malki Museum Press, Banning, CA.
Munz, P. A. 1959. A California flora. Univ. California Press, Berkeley.
Prose, D. V. and S. K. Metzger. 1985. Recovery of soils and vegetation in World War II military base camps, Mojave Desert. Open File Report. U.S. Geol. Survey, Menlo Park, CA.
Rowlands, P. G. 1980. Recovery, succession, and revegetation in the Mojave Desert. *In* P. G. Rowlands, ed., The effects of disturbance on desert soils, vegetation and community processes with emphasis on off-road vehicles: a critical review, p. 75–118. Spec. Publ., U.S.D.I., Bur. Land Management Desert Plan Staff.
Shreve, F. 1942. The desert vegetation of North America. Bot. Rev. 8:195–246.
——— and A. L. Hinckley. 1937. Thirty years of change in desert vegetation. Ecology 18:463–478.
Steel, R. G. D. and J. H. Torrie. 1980. Principles and procedures of statistics, 2nd ed. McGraw-Hill, New York.
Thompson, D. G. 1929. The Mojave Desert region, California: a geographic, geologic, and hydrographic reconnaissance. U.S.G.S. Prof. Paper No. 578. U.S. Gov. Printing Office, Washington.
U. S. Bureau of Land Management. 1971. Regulations pertaining to: disposition, occupancy and use—Desert Land Entries. Cir. No. 2291. U.S. Dept. Interior.
Vasek, F. C. 1979. Early successional stages in Mojave Desert scrub vegetation. Israeli J. Bot. 28:133–148.
———, and M. G. Barbour. 1977. Mojave Desert scrub vegetation. *In* M. G. Barbour and J. Major, eds., Terrestrial vegetation of California, p. 835–867. John Wiley & Sons, New York.
———, H. B. Johnson, and G. D. Brum. 1975a. Effects of power transmission lines on vegetation of the Mojave Desert. Madroño 23:114–130.
———, ———, and D. H. Eslinger. 1975b. Effects of pipeline construction on creosote bush scrub vegetation of the Mojave Desert. Madroño 23:1–13.
——— and L. J. Lund. 1980. Soil characteristics associated with a primary plant succession on a Mojave Desert dry lake. Ecology 61:1013–1018.
Webb, R. H. and H. G. Wilshire. 1980. Recovery of soils and vegetation in a Mojave Desert ghost town. J. Arid Environ. 3:291–303.
Wells, P. V. 1961. Succession in desert vegetation on streets of a Nevada ghost town. Science 134:670–671.

(Received 26 Apr 1985; revision accepted 5 Dec 1985.)